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VERTICILLIUM WILT OF STRAWBERRIES¹

HAROLD E. THOMAS²

During the past few years strawberry growers in California have become alarmed over the dying of plants. The trouble is assuming major importance in many strawberry plantings, particularly in the coastal districts of central California, but is by no means confined to this area. Some dying, either slow or outright, occurs in the majority of fields throughout the state and reports indicate that the dying out of plants is a trouble of some concern in many parts of the United States, Canada, Scotland, and England—as recorded by Frank,⁽⁴⁾ Neal,⁽⁷⁾ Coons,⁽⁸⁾ Sherbakoff,⁽¹¹⁾ Thomas,⁽¹⁴⁾ Plakidas,⁽⁹⁾ Walker,⁽¹⁶⁾ Strong and Strong,⁽¹²⁾ Wardlaw,^(17, 18, 19) Ball, Mann and Staniland,⁽²⁾ O'Brien and M'Naughton,⁽⁸⁾ and Alcock, Howells and Foister.⁽¹⁾ It must not be assumed, however, that death is due to the same cause in all regions nor that all plants in a given district are killed by the same agent.

The disease which forms the subject of the investigations herein reported, causes the plants to wilt, turn brown, and die, and because of the browning produced in the leaves of affected plants it has sometimes been referred to in California as "brown blight."^(5, 6) While this phrase is, in a measure, descriptive of the trouble and has been used by some growers, it is believed that "wilt" is a better term. The latter is one commonly employed by pathologists for diseases of this type and will be used in this report.

DESCRIPTION

The symptoms vary somewhat with the susceptibility of the variety affected and even within a given variety the effect on the individual plants may vary appreciably. Usually, but not always, the first sign of distress is a drooping or wilting of the outer leaves. In a severe case, on the more susceptible varieties such as Nich Ohmer or Capitola, the wilting may soon involve the major portion of the plant. The older leaves dry and either turn entirely brown or exhibit brown margins with a green center, water-soaked in appearance. The

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plant may die in a short time or linger for a period, forcing a few small leaves from the center of the crown and often one or more spindling side crowns. These eventually collapse and the plant dies. While the process is usually a gradual one, instances of sudden wilt have been noticed. At other times the plants may slowly die without exhibiting any definite symptoms of wilt.

In the varieties showing some resistance, the older, outermost leaves may wilt and eventually turn brown and die, but the younger center leaves remain alive, at least for some time. The affected plant assumes a reddish-yellow cast that readily distinguishes it from those not affected by the disease. If new leaves develop, they are usually small and chlorotic or yellow between the veins, and show a tinge of red in the veins. Often, from such plants, one to several side crowns are formed, giving the plant a bushy appearance. Affected plants, if not too severely attacked, may recover partially, live through the season, and start growth the following spring. Sufficient observations have not been made to determine whether or not such plants ever completely recover.

Wilt symptoms are caused at times by a decay in the base of the leaf stems or petioles. This condition should not be confused with the "wilt" under discussion as the cause is entirely different.

Roots are usually unchanged in external appearance by wilt. Plants which are affected soon after setting, but not killed outright, may fail to produce as large a secondary root system as would healthy plants, but those roots which develop are normal in appearance. It is only after the tops of affected plants have shown wilt symptoms for an extended period, or are largely or entirely dead, that the roots begin to break down. Browned and blackened roots are common on wilt-affected strawberry plants, but there seems to be no direct relation between these symptoms and the wilt disease.

Ordinarily there is no discoloration of the crown until the disease has reached an advanced stage. A few small brown spots may then be scattered through the fleshy portion. Definite darkening of the woody cylinder of the crown has not been observed.

Strawberry plants in California are normally set out between January 15 and May 1. It is usually not until July or later, when the plants are fully grown, with half or more of the runners set and the ground largely covered with foliage, that typical wilt symptoms appear in individual plants scattered through the planting. The number depends upon the degree to which the soil has previously become infested by the causal fungus and upon the susceptibility of

the variety. In heavily infested soil, plants continue to wilt and die during the summer and into the fall. Plantings of susceptible varieties have been observed with fully 75 per cent of the plants dead before the end of September while with the more resistant sorts, even though set in heavily infested soil, the number exhibiting wilt is noticeably less. Still more striking is the large number of the latter that show symptoms of disease but do not die.

Runners from infected mother plants may or may not die or show symptoms of wilt, depending partly upon whether or not the runners were established before or after the mother plant became seriously diseased. If runners are not established before the parent plant is seriously affected they will usually die owing to their failure to receive support from the latter. Runners, on the other hand, often wilt and die after becoming established, probably either because of a separate infection from the soil or through the stolon.

The "wilt" under discussion does not always differ essentially in aboveground symptoms from wilt due to other causes such as a lack of soil moisture, crown borers, and root or crown decay. While this may at times lead to confusion a careful examination of the whole plant will usually shed some light on the cause if it is due to one of these agents.

CAUSE

Repeated culturing from the crowns of wilting and dying plants from many strawberry fields usually yielded a species of *Verticillium* indistinguishable in its growth characteristics from *Verticillium albo-atrum* R. and B. as discussed by Rudolph⁽¹⁰⁾ in a recent review of the literature on diseases caused by *Verticillium* spp. This fungus has been reported as the cause of plant diseases in many states of the Union, in Canada, and in several countries of Europe. It is by no means a new one in California, having been known for some time as the cause of "blue stem" in raspberry, "blackheart" in stone fruits, and "wilt" in truck-crops.⁽¹⁰⁾ It has been particularly serious in coastal districts of California as the cause of wilt in tomatoes. Although Rudolph finds the disease reported on more than 120 species of plants in widely separated families, no record has been found of a *Verticillium* wilt of strawberry other than a very brief report by Van Poeteren⁽¹⁵⁾ in Holland, that an unidentified species of *Verticillium* (possibly *albo-atrum*) was cultured from a single completely withered strawberry plant. *Didymella lycopersici* was also isolated from the same plant. The former fungus was believed to be

the cause of the disease but no inoculation experiments were reported. It is believed that the present writer was the first to give any proof that *Verticillium* was the cause of a disease in strawberry.⁽¹³⁾

To study the causal relation of this fungus to the disease here described, 30 plants of the Nich Ohmer variety were inoculated on



Fig. 1.—*Verticillium* wilt of strawberry; inoculated and control plants of Nich Ohmer variety four months after planting. One-sixth actual size. Note stunted condition of inoculated lot. Older leaves are browned and dried.

January 12, 1931, by mixing either clover stem or agar cultures of the fungus with steam-sterilized soil and immediately setting the plants into this mixture in six-inch pots in the greenhouse. Twenty plants set at the same time, but receiving no inoculation, served as controls. The roots of all plants were cut back to about three inches imme-

dately before planting. On June 3 approximately 50 per cent of the inoculated lot exhibited symptoms of the disease. The remaining 50 per cent were for the most part free from these symptoms. *Verticillium* was isolated from several crowns of the diseased plants. It was not obtained from any of ten controls. Typically diseased and healthy plants of this experiment are shown in figure 1.

At the University of California Deciduous Fruit Field Station at San Jose, plants of the New Oregon (Marshall)³ and Nich Ohmer varieties were set on April 22, 1931, in soil that had been artificially infested with *Verticillium* the two preceding years and used for testing the resistance of tomato varieties.⁽¹⁰⁾ Typical symptoms of *Verticillium* wilt were present in the Nich Ohmer plants during the summer and fall. By the end of the season most of the plants of this lot had died. The New Oregon (Marshall) variety is less susceptible and only a small percentage died. Those remaining displayed evidence of infection by a wilting or browning of the outer leaves, a development of numerous side crowns, and the characteristic mild yellowing and reddening of veins. The casual fungus was isolated from several plants of each lot.

RELATION OF THE FUNGUS TO THE HOST

The assumption might naturally be made that *Verticillium* gains entrance to the plant through the roots and from the latter grows up into the other parts. It should therefore be expected that the fungus could be readily isolated from the roots of affected strawberry plants, but numerous attempts to do this have resulted in relatively few successful isolations. Of the several hundred roots taken from naturally infected plants from the field and cultured in the course of this investigation, no more than an occasional root yielded *Verticillium*. Only one colony of the fungus was obtained from the culturing of 95 roots of the artificially inoculated plants in the greenhouse.

Although *Verticillium* is isolated only with difficulty from the roots of affected plants it may be obtained readily from the crowns. It is more often cultured from the middle and upper portions of the crown than from the lower part. Of 45 affected crowns taken from

³ The varieties Banner, Oregon, New Oregon, and Oregon Plum, as grown in the various districts of the state, are believed by Darrow (Darrow, Geo. M., Strawberry culture: Western United States. U. S. Dept. Agr. Farmers' Bul. 1027. 1919. Revision in press.) to be the same, and synonymous with Marshall. To avoid confusion arising from the use of different names for the same variety, the name under which the plants were sold has been retained throughout this bulletin and "Marshall" added in parenthesis.

three fields, where a record was kept of the part of the crown from which cultures were made, *Verticillium* was obtained in 23.8 per cent of the cultures from the base of the crown, in 54.7 per cent of those from the center and in 56.8 per cent of those from the upper portion.

It was stated above that affected plants of the more resistant varieties usually form one to several side crowns. Culturing from the latter indicates that the fungus is usually present, though such crowns may be relatively small and display no external evidence of wilt other than at times a pale green color.

Limited data have been obtained on the occurrence of the fungus in the leaf petioles or stems. Culturing from 47 leaves taken from 3 affected plants having 3, 4, and 6 crowns respectively, demonstrated that the outer leaves from all the crowns had the fungus within the leaf petioles and it could be as readily isolated from the upper portion of the petiole as from the base. Only once did culturing from the young center leaves, having petioles $\frac{3}{4}$ inch or less in length, yield *Verticillium*. The leaves of intermediate position on the crown usually, but not always, contained the fungus in the tissues of the stems.

PREVALENCE AND IMPORTANCE

The disease has been found in several strawberry-growing districts in the state and it is reasonable to assume that in any section where *Verticillium* occurs on other crops, strawberries will become infected if set in the infested soil. In the limited amount of survey work done by the writer, the trouble was found most serious in the region around the San Francisco Bay and the Santa Clara and Pajaro valleys. This may be due partly to the fact that some of the more susceptible varieties are grown in these areas. It is also true that *Verticillium* in other crops is more serious in the coastal counties of the state.⁽¹⁰⁾ The trouble has been observed in scattered plants in the Stockton and Turlock districts where the Banner (Marshall) and Oregon (Marshall) are the principal varieties grown; but probably because of the resistance of these varieties the disease is not very serious in those districts. *Verticillium* was isolated from plants of the Klondike variety received from the Los Angeles section but no field studies have been made of the disease in that area.⁴

⁴ The nurseryman forwarding the plants from which the fungus was isolated states that the plants sent were typical of a trouble that is of major importance in the Los Angeles district.

In a letter to the writer Mr. D. G. Milbrath of the California State Department of Agriculture states that he found *Verticillium* fruiting on the leaves of strawberry plants sent in from Chino, San Bernardino County.

The most significant observation made by the writer on the prevalence of this disease is that of a striking correlation between the occurrence of *Verticillium* wilt on strawberry and the previous cropping of the land to tomatoes. In every strawberry planting showing very much injury by wilt, where the history of previous crops could be ascertained, tomatoes had been grown on the soil, usually preceding the strawberry planting by not more than one or two years. The tomato is known to be very susceptible to *Verticillium*. Either by



Fig. 2.—*Verticillium* wilt in a field of Capitola and Nich Ohmer varieties of strawberry causing a loss in plants amounting to over 50 per cent. The light-colored bare spots indicate areas in which the plants have died from wilt and have been removed. Old tomato vines were incorporated with the soil in the area shown on the right. The young cherry trees are unaffected by the disease.

setting wilt-infected tomato plants in clean soil, or through the ability of the fungus in a slightly infested soil to increase upon the susceptible tomato, the soil becomes heavily infested with *Verticillium* prior to setting the strawberry plants.

The losses incurred because of this disease vary greatly, according to the degree of infestation in the soil and the susceptibility of the variety of strawberries. A typical case bearing on the latter point was noted in the San Francisco Bay region where in a field of the Capitola variety the loss in plants the first season amounted to fully 75 per cent and the planting was practically ruined. In an adjoining field of Banner (Marshall) strawberries, separated from the

last by a pathway, the loss amounted to only an occasional plant. Both plots had received similar treatment. A field of the Capitola and Nich Ohmer varieties, in which more than 50 per cent of the plants were killed by the disease, is shown in figure 2.

Considering the state as a whole, wilt undoubtedly occasions an appreciable loss in strawberries and still greater losses may be expected in the future unless more care is exercised in selecting land free from the fungus for planting.

RELATION OF WILT TO ROOT TROUBLES IN CALIFORNIA

No direct relation appears to exist between the browning, blackening, and decay of strawberry roots, common in numerous plantings throughout this state, and the disease caused by *Verticillium*. It is a common observation that in strawberry fields an occasional plant may weaken and die. Frequently the dying is extensive, often confined more or less to spots. Examination of the plants in such areas may reveal partially decayed root systems, roots with numerous brown areas or surface lesions of varying size, roots with the cortex entirely blackened, decaying crowns, or a variety of defects of a similar nature. Such symptoms occur as frequently in plantings unaffected by wilt as in those in which wilt is extremely severe and it is believed the two troubles are distinct, although they may be associated in the same planting and at times in the same plant. Some of the browning and blackening of the root is the normal effect of age but there seems little doubt that a part of this condition must be attributed to causes other than normal aging. A variety of explanations such as the effect of alkali, excessive moisture in the soil, excessive drying and baking of the surface soil, excess of salts at the surface of the ground, and the effect of various fungi, have been advanced to account for the root troubles and the general decline of the plant. These agents undoubtedly have some effect but their relative significance has not as yet been evaluated.

Of some bearing on the relation between wilt and the darkening of roots are the observations made in the examination of the inoculated and control plants from the greenhouse. Counts were made on the number and condition of the roots coming from each of the plants examined. These are given in table 1.

It is evident that only very minor differences exist between the inoculated and control lots concerning the total number of roots per

plant and the proportion of these that exhibit lesions or blackening. It is extremely doubtful if these differences are at all significant. This lends support to the belief that wilt and the browning, blackening, and decay of roots are distinct troubles, but may be associated in the same plant.

TABLE 1
RELATION BETWEEN DARKENING OF ROOTS AND PRESENCE OF WILT FUNGUS

	Inoculated, and <i>Verticillium</i> isolated	Controls
Number of plants examined.....	11	10
Average number of roots per plant.....	31	34
Average number of roots per plant free from blackening or lesions.....	12	16
Average number of roots per plant blackened or exhibiting lesions.....	19	18

RELATION OF WILT TO STRAWBERRY ROOT TROUBLES REPORTED ELSEWHERE

Mention was made earlier of the dying of plants occurring in strawberry plantations outside of California. A brief discussion and comparison of wilt with related troubles reported by other investigators, is perhaps not out of place at this point. Some similarity of the symptoms produced in the top part of the plant may reasonably be expected to occur no matter what agent injures the root system. Wilting or dying is certain if water is prevented from reaching the leaves and similarities could be expected in these symptoms whether the effect is brought about by biological, mechanical, or other means.

Frank⁽⁴⁾ in 1920 reported the wilting and dying of strawberry plants in western Washington and believed *Rhizoctonia* the cause of the trouble. The symptoms which he briefly describes are not essentially different from those produced by *Verticillium*. Coons⁽³⁾ in 1924 associated *Rhizoctonia* with the black-root disease in Michigan. He considered poor soil, drainage and cultural conditions as factors favoring the trouble. More recent work by Strong and Strong⁽¹²⁾ indicates that the black-root disease in Michigan may be caused by either of two fungi, *Leptosphaeria coniothyrium* (Fekl.) Saec. or *Pezizella lythri* (Desm.) Shear and Dodge. The aboveground symptoms which they associate with the disease would lead one to believe that the injury described is much slower in developing than *Verticillium* wilt. The plants in Michigan slowly lose vitality through injury

to the root system.⁵ Neal⁽⁷⁾ in 1923 reports a root rot of strawberries in Mississippi. A *Fusarium* was isolated. He states, "The disease causes a distinct wilting of the plants accompanied by pronounced discoloration of the roots and crown tissue." The latter part of his statement distinguishes the trouble from wilt caused by *Verticillium*. A root rot of strawberries was reported by Sherbakoff⁽¹¹⁾ in Alabama and Tennessee. He did not identify the sterile fungus isolated. Thomas⁽¹⁴⁾ describes a disease affecting strawberry roots in New York state. In some respects it resembles *Verticillium* wilt but is probably slower in its effect on the plant. Several fungi were isolated but these were believed to be secondary in the production of injury. Plakidas⁽⁹⁾ was able to produce root injury in strawberries with a species of *Pythium*. No description of symptoms is given. Walker⁽¹⁶⁾ working in Ontario, Canada, describes a serious black-root condition. He believes *Ramularia* a factor but does not attribute the trouble to any one cause. The disease which he was investigating has many symptoms in common with the *Verticillium* wilt described in this bulletin. In studying the descriptions of these diseases one is struck by the marked similarity that exists between them although the conclusions reached by the individuals as to cause may be divergent.

Judging from the reports of the past several years serious root troubles occur in England and Scotland. The Lanarkshire strawberry disease of Scotland is probably the most serious, causing heavy losses each year. Field symptoms, as described by the several investigators of this trouble, are somewhat variable. The decline of the plant is usually gradual. The outer leaves die and turn brown. Symptoms of starvation are evident and the plant becomes stunted, if death is not outright. Seasonal variations in severity of symptoms exist. The disease is most active during the periods May to June and September to October. All investigators agree that there exists in diseased plants a paucity of fibrous roots. There seems to be little agreement as to the cause of this trouble. Wardlaw^(17, 18, 19) believed that species of *Pythium*, associated with excessive soil moisture, poor soil, and cultural conditions were responsible for much of the trouble. O'Brien and M'Naughton⁽⁸⁾ brought forward the novel idea that endotrophic mycorrhiza were responsible for the widespread dying of plants. They conclude that the mycorrhizal fungus (a phyeomycete) enters the fine fibrous roots, lives at the expense of the plant,

⁵ Since this bulletin went to press, a publication by Zeller (Zeller, S. M. A strawberry disease caused by *Rhizoctonia*. Oregon Agr. Exp. Sta. Bul. 295:1-24. 1932.) has been received. The author concluded that *Rhizoctonia solani* was the cause of a serious black-root disease in Oregon.

thus lowering the vitality of the roots, and at points on the finer rootlets, where extensive infection occurs, causes a rupturing of these rootlets. The latter are rendered non-functional and leave the plant with a greatly reduced absorbing root system. Death of the plant results in cases of severe infection. Other fungi may enter the weakened roots and intensify the disease. Alcock, Howells and Foister⁽¹⁾ in 1930 found a *Phytophthora* present in the roots of strawberry plants affected with the Lanarkshire disease and believed it to be the cause, but were unable to culture the fungus on artificial media. These authors consider the red core of diseased roots a diagnostic symptom of the trouble and one that may be used in the field to identify this particular disease.

In England, Ball, Mann and Staniland⁽²⁾ classify a trouble occurring there as "sudden wilt." It is characterized by a rapid wilting of the plant usually occurring about the time that fruit is fully formed. The plant may either subsequently die or become a small-leaf type. Fungi have been isolated but are not considered to be the cause of the trouble. A form of localized water-logging may be responsible at times, and root-feeding insects at other times.

The foregoing discussion emphasizes the fact that there are many troubles affecting strawberry roots. It may be pointed out that many of the symptoms produced by these troubles are similar in appearance. How many of these various diseases described in the literature may eventually be shown to be of common origin is a problem for the future. *Verticillium* is a fungus of widespread occurrence and has been reported on numerous hosts from sections where strawberries have been or are being grown. It is surprising that hitherto only one recorded account of this fungus on the strawberry has been found,⁽¹⁵⁾ and in that instance the fungus was cultured from only one plant.

CONTROL

No specific recommendations for control of *Verticillium* wilt can be made but certain factors of some value in combating the disease and its spread may be suggested.

No evidence exists at the present time that plants coming from the various propagating nurseries are infected with the wilt fungus upon arrival. On the other hand, it is not unlikely that plants could become infected in the propagating bed and spread the disease into the field. Those engaged in propagating plants for sale should be careful that their beds are located on ground not previously cropped to tomatoes or other plants known to be affected with *Verticillium* wilt.

Resetting healthy plants where the diseased plants have been removed is of very questionable value; the chances are great for infection of the newly set plant because of the infestation already in the soil.

To plant strawberries on any land known to have been cropped with plants affected with *Verticillium* is very poor policy and trouble may be expected. If the infested soil has produced crops of non-susceptible plants for a few years previous to setting strawberries, the latter may suffer but little injury. How long such a period of cropping is necessary, to eradicate the fungus, will vary with circumstances and not enough data are at hand to make any general recommendations. The fungus is apparently capable of living for some time in uncropped soil.

Following is a list of the more susceptible common crops⁽¹⁰⁾ that should not be used in a system of crop rotation designed to rid the soil of *Verticillium*: tomato, potato, beet, cucumber, eggplant, melon, pepper, raspberry, blackberry, and dewberry. Several of our common fruit trees (almond, apricot, prune, peach) are subject to this disease, and strawberries should not be planted on land recently cleared of trees suffering from *Verticillium* wilt.

From the field observations made thus far it is concluded that the tomato is the principal crop responsible for the spread of the fungus to strawberry and several years should elapse between the growing of tomatoes and the planting of strawberries. Not all tomato plantings are affected by wilt but symptoms are at times so indefinite that this crop should be avoided where it is intended that strawberries shall be planted; at least until it is better understood why *Verticillium* is so constantly spread in the field through the practice of growing tomatoes.

Spraying is of no avail in the control of this disease.

Plants showing symptoms of wilt are sometimes thought to be suffering from lack of moisture and often greater amounts of water are added. This usually not only fails to improve the condition in the plant but actually aggravates the disease.

In the field there exists a striking variation in the susceptibility of varieties and sufficient resistance is exhibited by some to indicate the possibility of developing highly resistant commercial varieties. At the present only meager data taken from the field are to be had and it should be realized that any statement concerning varietal resistance is necessarily provisional. Nich Ohmer and Capitola (fig. 3) are very susceptible while the varieties of the Marshall type (Banner, Oregon, Oregon Plum) (fig. 4), and also the Klondike and Blakemore, appear

to be comparatively resistant. Superb, Mastodon, and Missionary are apparently susceptible but too few observations have been made on these varieties.

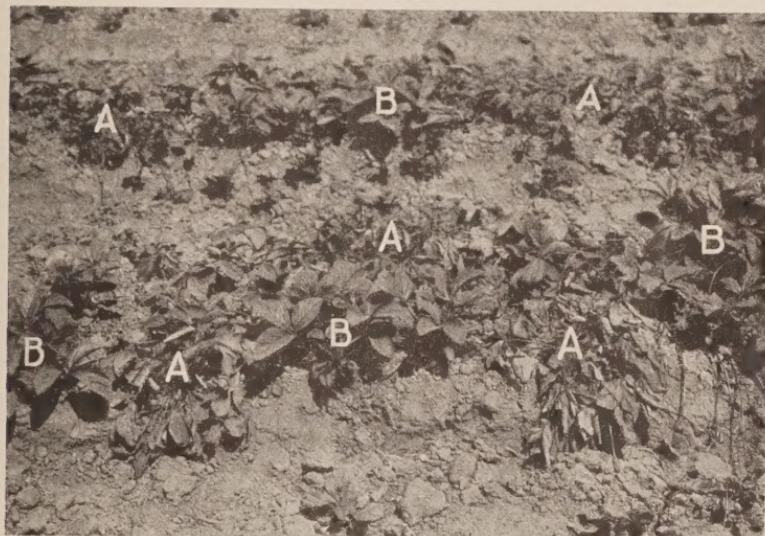


Fig. 3.—*Verticillium* wilt in the susceptible Capitola strawberry. Wilted plants at *A*; healthy at *B*.



Fig. 4.—*Verticillium* wilt in the resistant Banner variety of strawberry. The affected plant is shown at the center. Only the outer leaves are wilted and browned.

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